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MORPHOLOGICAL EVIDENCE OF HYBRIDIZATION
BETWEEN ARCTOSTAPHYLOS GLAUCA AND
A. PUNGENS (ERICACEAE)

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Arctostaphylos is a large genus of evergreen shrubs common in western North America. Although species in the group occupy various habitats throughout this region, their greatest diversity is found in the chaparral covered coastal ranges of California. The diversified topography of this area, with its exceedingly complex mosaic of habitats, has doubtlessly contributed to the diversity of the group. Jepson (1939) suggested that much of the variation in this genus was associated with minor climatic differences and was related to the geological history of the region. Similar factors have been proposed by Gankin and Major (1964) to account for the origin of *A. myrtifolia* Parry, and Vasek and Clovis (1976) have also suggested that recent climatic selection has resulted in a complex pattern of variation in *A. glauca* Lindl.

Hybridization has been implicated in explanations of variation in at least 30 species, subspecies, or varieties (Baker, 1932; Eastwood, 1934, 1937; McMinn, 1939; Jepson, 1939; Adams, 1940; Howell, 1955; Munz, 1959; Roof, 1962; Hoover, 1964; Gankin and Hildreth, 1964; Gankin, 1966; Wells, 1965, 1968, 1972). Despite the frequency of reports of suspected hybridization in *Arctostaphylos*, relatively little biosystematic evidence for it has been published. Epling (1947) made the first attempts by quantifying leaf proportions along a transect from a stand of "pure" *A. mariposa* Dudl. in Eastw. to a stand of "pure" *A. patula* Greene. He, and later Dobzhansky (1953), concluded that although hybrids between these two species were abundant and vigorous, both species remained quite distinct along the zone of contact. More recent and complete studies have clearly indicated hybridization between *A. nissenana* Merriam and *A. viscida* Parry (Schmid et al., 1968) and between *A. viscida* and *A. canescens* Eastw. (Gottlieb, 1968). The results of the latter study led Gottlieb to conclude that several species maintained in standard floras are hybrids.

The purpose of this study was to document phenetic patterns of a putative hybrid swarm between *A. glauca* and *A. pungens* HBK., with a view to answering two questions: 1) is there an apparent recombinant type emerging from this population? 2) is there any detectable introgression from one species to the other?

Both *A. glauca* and *A. pungens* are well-defined, easily recognizable, diploid ($2n = 26$), non-burl-forming shrubs that often reach arborescent proportions. *Arctostaphylos glauca* has glaucous ovate leaves 2.0–4.5 cm long with truncate or subcordate bases, petioles 7–10 mm long. Inflorescences are long, narrow, and much branched. Petioles, branchlets, and rachises are typically glabrous and glaucous. Fruits are the largest found in the genus, 12–15 mm in diameter, globose, viscid, and borne on densely glandular pedicels. The exocarp is thin and leathery, there is no mesocarp, and the hard resin-like endocarp is fused into a smooth, solid, apiculate stone enclosing 5–6 seeds. *Arctostaphylos pungens* has narrowly elliptic to almost lanceolate leaves 1.5–3.0 cm long with acute bases, and petioles 3–4 mm long. Inflorescences are short, few branched, and broadened at the tip. Petioles, branchlets, and rachises are densely canescent. Fruits are glabrous, depressed-globose, 5–10 mm broad, and borne on glabrous pedicels. The mesocarp is a mealy pulp and the resin-like endocarp is divided into 5–6 distinct nutlets.

Arctostaphylos glauca is common on dry slopes in chaparral from Baja California through the inner Coastal Ranges to Contra Costa Co., California. *Arctostaphylos pungens* is common from the Mexican Highlands through southern Texas and frequently in higher elevation chaparral and woodland from southern California north to San Benito Co., California (Munz, 1959). In the mountains east of San Diego, *A. glauca* is a common component of chaparral between 600 m and 1500 m. *Arctostaphylos pungens* is frequent in oak woodlands at about 800 m. It becomes more common in chaparral at higher elevations and extends into yellow pine forest up to 2000 m. These two species seldom occur together, although *A. glauca* is found throughout this region in close association with *A. glandulosa* Eastw., a hexaploid, burl-forming shrub.

STUDY SITES AND METHODS

The putative hybrid swarm is in Echo Valley (1000 m), ca 8 km N of Descanso, San Diego Co., California. Here *Arctostaphylos pungens* is scattered among *Quercus agrifolia* Neé in flat areas of the valley bottom while *A. glauca* is common on slopes in association with *A. glandulosa*, *Adenostoma fasciculatum* H. & A., *Quercus dumosa* Nutt., *Ceanothus leucodermus* Greene, and *C. greggii* Gray var. *perplexans* (Trel.) Jeps. In one ravine, on the north-facing slope, *A. glauca* and *A. pungens* occur together with shrubs that combine characteristics of both of these species. This area had not burned in at least 20 years and no obvious disturbance was evident.

Samples were taken by walking a straight line through the center of

the population and collecting a fruiting branch from each of the first 40 shrubs encountered (*J. Keeley 4110-4149*). A similar procedure was used to sample populations of "pure" *A. pungens* and "pure" *A. glauca* except that a sample size of 15 was used. The *A. pungens* population was about 200 m S of the putative hybrid population and the *A. glauca* population was from the east end of Willows Road, The Willows (850 m), ca 9 km SW of Echo Valley. The *A. glauca* population was sampled in Aug 1973 and the *A. pungens* and the putative hybrid populations were sampled in Aug 1974. Vouchers will be deposited in SD.

Each specimen was scored as follows: Ten leaves were randomly selected and removed; leaf length and width and petiole length were measured. The angle (from the midrib) of the leaf base was measured for three leaves. Five inflorescences were selected and the number of side branches recorded, and length of the rachis and width near the tip of the rachis was recorded. Ten fruits were scored as follows: after oven drying to constant weight, the fruits were (1) weighed, the outer pericarp (exocarp and mesocarp) was removed by rubbing on a wire screen, (2) the number of segments into which the endocarp broke was recorded, and (3) these segments were weighed.

The mean value for each of these characters was recorded. Meristic characters (number of inflorescence side branches and number of endocarp segments) were expressed as real numbers. In addition to these quantitative measurements, each specimen was qualitatively scored for: glaucousness (presence of a whitish bloom on the leaves), glandularity, and type of, or absence of, indument on the branchlets, inflorescences, pedicels, and fruits.

Using these data, scatter diagrams were constructed from values for the major distinguishing characteristics. In order to show how shrubs in the hybrid population combined characteristics, a hybrid index similar to that of Anderson (1949) was developed. Rather than sorting quantitative data into discrete groups (e.g., 0 for one parent, 2 for the other, and 1 for intermediates), the following procedure was used. The specimen that had the largest mean measurement for a character was given a value of 1 for that character and all other specimens were scaled proportionately for that character. An *A. glauca* specimen had the largest measurement for most of the characters studied. For those characters in which *A. glauca* did not have the largest measurement, the inverse of the scaled measurement was used. It was thought that this method would make the index more objective as well as more sensitive to gradual changes in the phenetic characters examined.

Ten quantitative characters were used for the hybrid index: leaf length, leaf width/length ratio, petiole length, angle of leaf base, length of inflorescence rachis, width near rachis tip, number of inflorescence side branches, fruit (minus outer pericarp) weight, percent (by weight) of fruit as outer pericarp, and number of endocarp segments. In addition, four qualitative characters (leaf bloom, branchlet indument, glandularity

of pedicels, and glandularity of fruits) were used by assigning values of "0" for *A. pungens*-like, "1" for *A. glauca*-like, and "0.5" for anything else.

RESULTS AND DISCUSSION

Recombination of characteristics of *A. glauca* and *A. pungens* in the shrubs from the Echo Valley population is clearly documented in the scatter diagrams (figs. 1 and 2). Nearly all of the shrubs in this population either had characteristics that were intermediate between those of *A. glauca* and *A. pungens* or had combinations of characteristics of both species.

The hybrid index histogram (fig. 3) also illustrates the hybrid nature of the Echo Valley population. Most of the 40 shrubs that were examined at this site had hybrid index values that fell between those of *A. glauca* and *A. pungens*. Also, there was a noticeable scarcity of intermediate values (7-8). Thus, assuming "F₁" individuals would be intermediate between the two parents, it would appear that this population is composed predominantly of backcrosses to either *A. pungens* or *A. glauca*. However, confirmation of this conclusion would require information on the genetics controlling these traits, and this sort of data is difficult to obtain for woody plants.

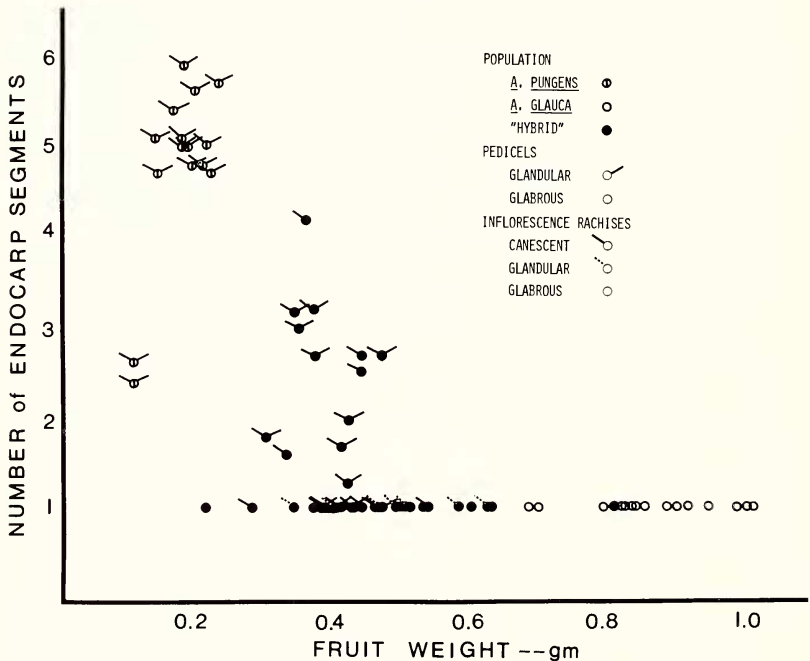


FIG. 1. Pictorialized scatter diagram of the "pure" *Arctostaphylos pungens* population, the "pure" *A. glauca* population, and the putative hybrid population.

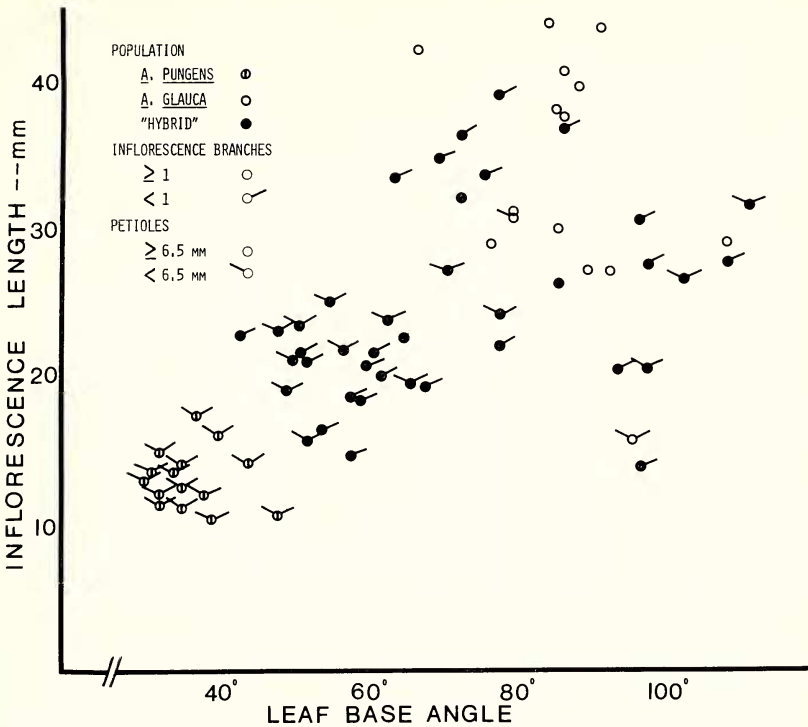


FIG. 2. Pictorialized scatter diagram of the "pure" *Arctostaphylos pungens* population, the "pure" *A. glauca* population, and the putative hybrid population.

The wide distribution of values in the hybrid index histogram (fig. 3) indicates that there are several different recombinant types in the hybrid population. The diversity is even more pronounced than is shown by Figure 3; many of the specimens with the same hybrid index value had very different combinations of characteristics. However, there was a single recombinant type in high frequency with respect to fruit characteristics (fig. 2). A large proportion (ca 70%) of the shrubs in this population had small (*pungens*-like) fruits with "nearly" or completely fused endocarp segments (*glauca*-like). This finding is interesting in light of the occurrence of the fused endocarps in the genus; only six other species in the group have this trait. All six have fruits smaller than those of *A. glauca* and are endemic within the range of overlap of *A. glauca* and *A. pungens*.

The clear discontinuity between the *A. pungens* population and the hybrid population in Figures 1, 2, and 3, indicates that there has not been any introgression of *A. glauca* characteristics into *A. pungens*. However, the occurrence of shrubs in the hybrid population with characteristics that fall within the range of variability of *A. glauca*, but have one or two traits of *A. pungens* (figs. 1, 2, and 3), suggests that there has

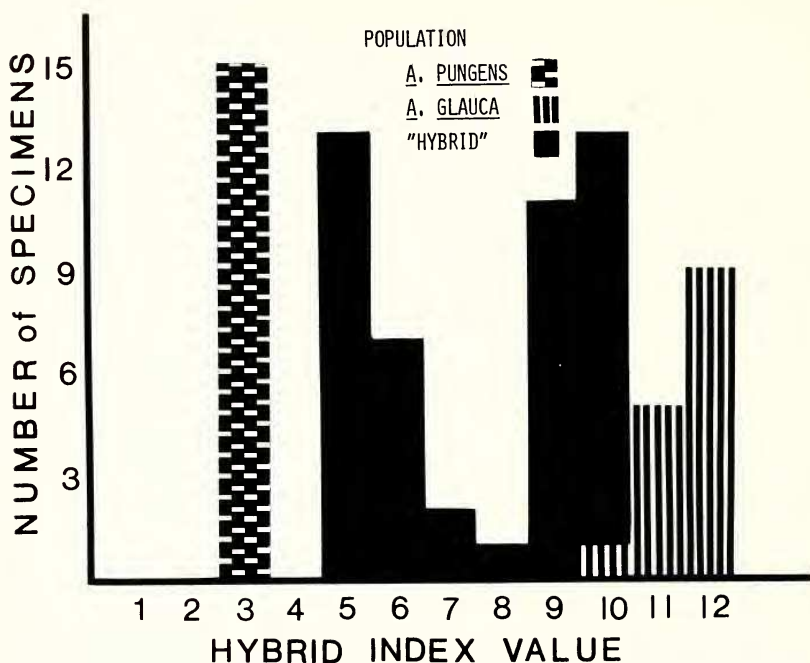


FIG. 3. Histogram of hybrid index values for the "pure" *Arctostaphylos pungens* population, the "pure" *A. glauca* population, and the putative hybrid population.

been introgression of *A. pungens* characteristics into *A. glauca*. In order to examine what effect introgression may have on *A. glauca* away from this immediate area, the following sampling was undertaken. On an east-facing slope about 100 m away, 30 *A. glauca* shrubs were scored for being glauca-like or pungens-like for six characters. Although *A. pungens* is very rare on this slope, only 13 percent of the *A. glauca* shrubs were scored as glauca-like for all six characters. Sixty percent of the shrubs had two or more pungens-like characteristics. Thus, it appears that there is introgression of genes from *A. pungens* into *A. glauca*, and it is detectable away from the site of active hybridization. Whether this is "true" introgression, i.e., a permanent addition of genes into the gene pool (Stebbins, 1959) is not known.

The results of this study indicate that *Arctostaphylos glauca* and *A. pungens* can hybridize when in close proximity to one another. It appears that the Echo Valley hybrid population is composed mainly of backcrosses to both parents. In addition, introgression of *A. pungens* genes into the gene pool of *A. glauca* is suggested by the occurrence of "*A. glauca*" shrubs with one or several *A. pungens* characteristics. Although most of the data from this study can be interpreted by simple explanations such as these, the occurrence of several hybrids with glandular-puberulent petioles, branchlets, and inflorescences, characteristics

of neither *A. glauca* nor *A. pungens* (fig. 2), cannot be easily explained. There are a number of sources by which these traits may have arisen. They may be: (1) the result of new gene combinations, a phenomenon that has been shown for both morphological and chemical characters in some hybrids (Turner and Alston, 1959), (2) the result of hybridization with *A. glandulosa*, a species with glandular petioles, branchlets, and inflorescences and also common at the Echo Valley Site, or (3) the result of introgression with *A. glauca* var. *puberula* J. T. Howell, which differs from var. *glauca* only in its glandular petioles, branchlets, and inflorescences and has recently been reported from several localities near Echo Valley (Keeley, 1975). Alternatively, the origin of var. *puberula* may be linked to one or both of the first two hypotheses. Investigation of this problem would perhaps reveal a great deal about the role of hybridization and introgression in the complicated pattern of variation in this genus.

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SYSTEMATIC POSITION OF REDFIELDIA (GRAMINEAE)

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In a recent paper reporting on his studies of leaf anatomy among members of the Eragrostoideae, Sutton (1973) indicated that *Redfieldia* Vasey does not belong in this group. As a result of his investigations, he concluded that this genus "should be left in the Festucoideae (tribe Festuceae) as placed by Hitchcock (1935)". Curiously, he did not note that the Grass Manual was revised in 1951 by Mrs. Agnes Chase and that in the later edition, *Redfieldia* is still retained in the Festuceae. It should also be pointed out that Vasey (1887) indicated that it appears to be related to *Festuca*.

Aside from the work of Sutton referred to above, the only other anatomical investigation of *Redfieldia* appears to be that of Decker (1964). In this latter publication the author did not discuss *Redfieldia*, but listed it in his table. Decker indicated that the genus is clearly eragrostoid in all characteristics including those observed in transections of the leaf blade. It is noteworthy that although Sutton listed the above paper in his bibliography, he did not point out that Decker's conclusions were in direct contrast to his own.

Redfieldia was described to accommodate a single species of sand-binding grass originally collected by Hall and Harbour in 1862. It had been recognized as a new species by Thurber, who in 1863 gave it the specific epithet *flexuosum* and doubtfully assigned it to *Graphephorum*